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The fate of glucose, a low molecular weight compound of root exudates, in the belowground foodweb of forests and pastures

Michael S. Strickland [a,*], Kyle Wickings [b], Mark A. Bradford [a]

[a] School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA
[b] Natural Resources and the Environment, University of New Hampshire, Durham, NH 03824, USA

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ABSTRACT

Increasing evidence suggests that much of belowground, heterotrophic activity in terrestrial ecosystems is fueled by inputs of low molecular weight carbon compounds (LMWCCs). Root exudation (rhizodeposition) is a primary source of these inputs and will likely increase with rising atmospheric CO_2. Yet the fates of these compounds belowground, as well as the environmental factors that influence them, are relatively unexplored. Using stable isotopes we track the fate of one dominant LMWCC, glucose, in three pasture and three forest sites located in South Carolina, USA. We resolve glucose-derived C in CO_2, dissolved and soil organic C (DOC, SOC), microbial biomass, and microarthropods (Collembola, oribatid and mesostigmatid mites). After 72 h, the greatest proportions of glucose-C are in microbial biomass and SOC, followed by CO_2, DOC, and microarthropods. Within this short time frame, glucose-C propagates through the foodweb to the highest trophic level, predatory mesostigmatid mites. The biomass of these predators is the only variable that explains the relative partitioning across sites of glucose-C, with higher biomass associated with reduced partitioning of glucose-C to respiration and hence greater retention belowground. Our results suggest that LMWCCs entering belowground systems may propagate through soil foodwebs rapidly, and that their partitioning belowground may potentially be determined by higher trophic levels.

1. Introduction

Low molecular weight carbon compounds (LMWCCs), composed of sugars, organic acids, and amino acids, are some of the most reactive forms of carbon (C) entering the belowground in terrestrial ecosystems (Yang and Janssen 2002, van Hees et al., 2005; Boddy et al., 2007). Indeed, they may fuel the bulk of microbial growth and activity and account for as much as 30% of total soil respiration (van Hees et al., 2005). In doing so, they play both a direct and indirect role in the formation, decomposition and stabilization of soil C stores, the regulation of nutrient cycling, and the provision of energy to belowground foodwebs (Dakora and Phillips 2002; van Hees et al., 2005; De Graff et al., 2010). They are primarily derived from recent photoassimilate that enters the belowground in dissolved form through root exudation (van Hees et al., 2005; De Graff et al., 2010; Strickland et al., 2010; Phillips et al., 2011). Their initial residence in the dissolved organic C (DOC) pool is on the order of hours, and from there they are either sorbed to soil surfaces or assimilated by the microbial biomass (Saggar et al., 1999; van Hees et al., 2005; Boddy et al., 2007; Fischer et al., 2010). Given this rapid removal of LMWCCs from the DOC pool, their fate is typically accounted for in respired C, microbial biomass, DOC, and soil organic C (SOC), and more often as only what is respired versus what remains in the soil (Fig. 1) (Fischer et al., 2010). This accounting does not resolve the potential for trophic interactions such as microbivory and predation to influence the fate and partitioning of LMWCCs belowground, despite the potential role of such interactions in regulating above and belowground foodweb and C dynamics (Bonkowski, 2004; Bradford et al., 2007; Hawlena and Schmitz, 2010a,b; Wickings and Grandy, 2011).

Studies tracking the fate of photoassimilate show that soil animals, specifically microarthropods, derive a substantial proportion of their C from recently, photosynthetically-fixed C (Pollierer et al., 2007; Bradford et al., 2007; Högberg et al., 2010). Undoubtedly, some of this C enters the belowground as LMWCCs through root exudation (Dakora and Phillips 2002; De Graff et al., 2010; Pollierer et al., 2007), but much of the C may also enter through other pathways (e.g., herbivory) and in other forms (e.g., frass). This means that to understand the specific fate of LMWCCs requires studies that track individual LMWCCs belowground. Glucose, a dominant

* Corresponding author.
E-mail address: michael.strickland@yale.edu (M.S. Strickland).

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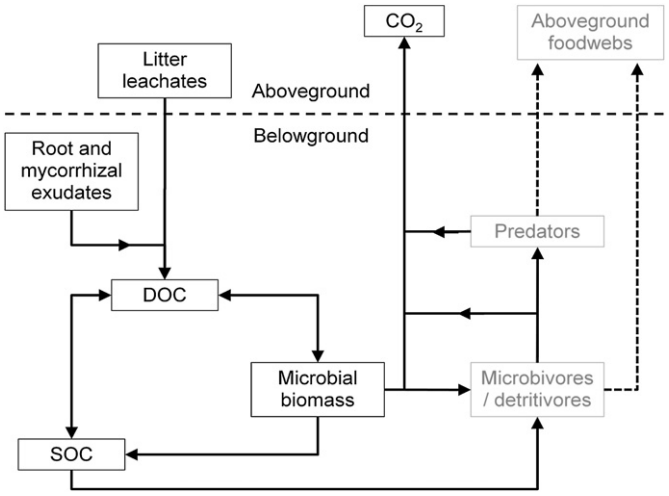

Fig. 1. Conceptual diagram showing the fate and expected pathways of LMWCCs belowground. Generally, these compounds have been tracked in respiration, DOC, SOC and microbial biomass C. However, as these compounds likely fuel a significant proportion of microbial activity, it is also likely that they will enter higher trophic levels in soils and ultimately aboveground systems (indicated in gray). Although these trophic pathways have been explored for C fixed via photosynthesis, they have not been explored for specific LMWCCs.

LMWCC in DOC and exudates (van Hees et al., 2005; De Graff et al., 2010), is commonly used for such tracking experiments but its partitioning in belowground foodwebs is largely unknown. Some common expectations are that the bulk of C derived from LMWCCs will be respired through microbial activity, incorporated into microbial biomass, or sorbed to soil surfaces (Saggar et al., 1999; van Hees et al., 2005; Fischer et al., 2010). Given that most LMWCCs can be assimilated by the microbial biomass, variation in partitioning is often considered to be driven primarily by characteristics of the microbial community (i.e., size, activity, and composition) (van Hees et al., 2005; De Graff et al., 2010; Strickland et al., 2010). Yet research on isotopically-labeled photoassimilates indicates the potential for LMWCCs to rapidly (i.e., days) enter a range of belowground pools from sporocarps to microarthropods (Pollierer et al., 2007; Högberg and Read 2006; Högberg et al., 2008, 2010; Wu et al., 2009). There is also some indication that factors besides those directly related to the microbial community, such as soil nutrient status and land management, influence the partitioning of LMWCCs belowground (Strickland et al., 2010). To better understand the partitioning of LMWCC belowground, and the environmental factors that influence it, requires field investigations that track inputs of specific LMWCCs into belowground C pools and foodwebs.

The objective of this study was to resolve the fate of glucose-C, a common LMWCC often found in root exudates, in the belowground C pools of forests and pastures. We achieve this objective by tracking ^{13}C labeled glucose into soil C (DOC and SOC) and belowground foodwebs as well as soil respiration (CO_2). We also sought to better understand what soil chemical, physical, and biological factors might influence or are at least related to the partitioning of this addition of glucose-C belowground.

2. Methods

2.1. Site description

In June 2007, we conducted a ^{13}C-glucose pulse-chase experiment in three pasture (P1–P3) and forest (F1–F3) sites near the Calhoun Experimental Forest, South Carolina, USA (approx. 34.5°N, 82°W). Pastures are fertilized, limed, cattle-grazed and rye (*Lolium* sp.) and Bermuda (*Panicum* sp.) grasses are the dominant plant cover. Forests are ~75 y old oak-hickory (*Quercus* sp. and *Carya* sp.) stands with minimal understory species composed in part of American Holly (*Ilex opaca*) and Virginia creeper (*Parthenocissus quinquefolia*). One forest site (F2) is grazed by cattle. Soils at these sites are acidic Ultisols classed as fine, kaolinitic, thermic Typic Kanhapludults of the Appling, Cecil, Hiwassee, and Madison series (Callaham et al., 2006). Average bulk densities (for depth 0–7.5 cm) ± 1 S.E. are 1.66 ± 0.10 and 1.16 ± 0.17 g cm^{-3} for pasture and forest sites, respectively. Average soil pH ± 1 S.E. are 5.13 ± 0.09 and 5.17 ± 0.28 for pasture and forest sites, respectively. Mean SOC content (g m^{-2} to 7.5 cm depth) ± 1 S.E. for forests are 1670.5 ± 317.7 and pastures are 1221.5 ± 29.5. All forest soils and P1 are sandy loams and the other pasture soils are loamy sands (Strickland et al., 2010). All sites are within 12 km of each other and are located on uplands with minimal slope and on interfluves from similar bedrock (i.e., granitic-gneiss). Thus, we attempted to control for native soil characteristics, geomorphology, and geology. See Strickland et al. (2010) and Table 1 for further site details.

The pasture and forested sites represented two distinct land cover types within the Calhoun Experimental Forest, specifically, and the Southeastern United States, in general, that differ both in their contemporary and historic management regimes (Richter et al., 1999; Richter and Markewitz, 2001). Due to these contemporary and historic management regimes these sites are representative of the variation in soil chemical, physical, and biological characteristics associated with soils in the Southeast and for this reason it should be noted that this was not a controlled study solely aimed at examining differences between land management regimes. It was an observational study aimed at understanding the potential characteristics of a site, including the contemporary management regime, that may influence the partitioning of low molecular weight C compounds belowground and more often than not pastures and forests represented the extremes in many of these characteristics.

2.2. Tracking ^{13}C-glucose

To track ^{13}C-glucose we used the approach described in Strickland et al. (2010). Briefly, two PVC collars (15.4 cm dia., inserted 5 cm into the soil) were placed at each site (i.e., analytical replicates) and, the day prior to glucose additions, water (1 L) was added to each collar to minimize differences in water potentials across collars. Then, 99-atom% ^{13}C-glucose (1 L of 2.5 mM solution) was added to each collar. The amount of C added was small (<25 μg C g dry weight $soil^{-1}$ in the top 7.5 cm), representing <0.0001% of total soil C. The glucose addition drained for 2 h and then soil respiration was tracked across 72 h. Soil respiration was measured using a closed-chamber technique, and initial samples (i.e., prior to glucose addition) gave natural abundance values for CO_2 produced. A gas sample was taken immediately after sealing each PVC collar with a cap fitted with a septa, and 45 min post sealing, using a 20 mL SGE gas syringe. Samples were transported back to the lab (located in Athens, GA, USA) in evacuated 12 mL Exetainers where total CO_2 concentration was determined on an infrared gas analyzer (IRGA; Li-Cor Biosciences, Lincoln, NE, USA, Model LI-7000) and $^{13}CO_2$ was determined using isotope-ratio mass spectrometry (IRMS; see below).

After 72 h soil contained within the entire PVC collar was harvested to 7.5 cm depth, divided into halves, with one half sieved (4 mm) before DOC, SOC, and microbial biomass C determinations, and the other half lightly crumbled by hand, to ensure even drying in the Tullgren funnels, for microarthropod extractions. Microbial biomass C and DOC were determined using the modified